Chapter 6

Herpetofauna of Montane Areas of Tanzania. 2. Altitudinal Distribution of Amphibians on the Uluguru South Mountains

Wilirk Ngalason¹ and Felix J. Mkonyi²

¹Department of Zoology and Wildlife Conservation, University of Dar es Salaam, P.O. Box 35064, Dar es Salaam, Tanzania ²Department of Biological Sciences, Dar es Salaam University College of Education, P.O. Box 2329, Dar es Salaam, Tanzania

Abstract

We present data on the altitudinal distribution of amphibians on the western slopes of Uluguru South Mountains, Tanzania. These mountains form part of the Eastern Arc Mountains, which are known for their biodiversity richness. We used drift fences with pitfall buckets, plots, and audio-visual survey methods. A total of 21 species was found during the survey. Four species previously reported in the Uluguru South Mountains were not found during the present survey. Generally, the number of species was highest at lower altitudes and decreased with increased altitude. Species similarity index showed that the study sites adjacent to each other had greater similarity in amphibian species composition than did sites distant from each other. The Uluguru Mountains are characterized by altitudinal variation in vegetation types and climatic factors such as temperature and rainfall, which may affect the distribution of amphibians on the mountain.

Introduction

The distribution of animal species largely relates to their habitat requirements. The primary environmental factors that limit the distribution of species include climate, topography, vegetation type, microhabitat, soil, and geology (Davis et al., 1990; Heyer et al., 1994). Linked to changes in environmental factors is altitude, and this parameter is often used for examining the distribution and richness of species across habitats. Changes in the richness of amphibians across altitudinal gradients have been examined across the globe (e.g., Fauth et al., 1989; Owen, 1989; Buckley & Jetz, 2007). Declines in amphibian diversity with increases in altitude correspond to changes in environmental factors, wherein areas with less favorable conditions support fewer species (Poynton, 1962).

Generally, the distribution of amphibians along an altitudinal gradient is not uniform (Brown & Alcala, 1961; Scott, 1976; Heatwole, 1982). There appear to be some discrete "cutoff points" at which the lowland species are separated from those in the upland areas. Studies of southern and East African lowland and mountain systems have shown species turnover, changing between different areas with climatic variations that determine these cut-off points (Poynton, 1990, 1992, 2000, 2003; Loader et al., 2004).

The Uluguru Mountains form part of the Eastern Arc Mountains, which are a chain of isolated crystalline mountains running from southern Kenya through Tanzania in a crescent-shaped arc (Lovett, 1990). The Eastern Arc Mountains form one of the global biodiversity hotspots due to their high species diversity (Myers et al., 2000), a consequence of factors including fragmentation associated with altitude, zonation of climate, and altitudinal turnover in species composition (Poynton et al., 2006). The Uluguru Mountains are divided into Uluguru North and Uluguru South. They rise to about 2600 m above sea level on the Lukwangule Plateau. The lower slopes, from 600 to about 1600 m, have been deforested, whereas the mid-altitude portions are still covered by degraded forest. The only intact portion is located on the higher altitudes above 2000 m. Annual distribution of rainfall and dry season length are the main climatic factors determining forest limits in the Eastern Arc Mountains, with the exception of frost, which determines the upper altitudinal limits (Lovett, 1993). Forests in the Uluguru Mountains are divided into lowland (below 500 m), submontane (800– 1500 m), montane (1500–1850 m), and upper montane forest (1850–2400 m) (Pócs, 1976a, b, c). Above the forest limits are heath and grassland vegetation on the Lukwangule Plateau.

The Uluguru Mountains are characterized by an oceanic rainfall pattern. The mountains receive short rains (*Vuli*) from October to December and the heavy long rains (*Masika*) from March to May. Estimated rainfall on the eastern slopes of Uluguru South is 2500–4000 mm/year, whereas on the western slopes, rainfall is estimated at 2000 mm/year. Mist and clouds occur throughout the year and are important sources of dry season moisture in higher altitude forests (Pócs, 1976a). The mean annual temperature in the Uluguru South is about 24.3°C with small seasonal variation. At lower altitudes, mean temperature ranges from 21.1°C to 26.5°C, whereas frost occurs above 2100 m in the Uluguru Mountains (Pócs, 1976b).

The altitudinal distribution of African amphibian fauna is well studied in southern Africa. Some of the comprehensive broad-scale studies in the altitudinal distribution of amphibians in Africa include those by Poynton and Broadley (1991), Poynton and Boycott (1996), and Poynton (1992, 2003). In the Uluguru Mountains, the earliest inventory was carried out by Barbour and Loveridge (1928). Subsequent studies were carried out by Doggart et al. (2004) followed by other collectors (mainly Frontier Tanzania). Despite these studies, there has been little effort to determine the altitudinal distribution of amphibians in the Uluguru Mountains. This study attempts to determine the altitudinal distribution of amphibians in the Uluguru South Mountains. The core data used in this study come from an altitudinal transect that was established on the western slopes of this range. The paper also reviews what is known of the Uluguru South Mountains.

Materials and Methods

Amphibians were studied along an altitudinal gradient on the western slopes of the Uluguru South Mountains from 1000 m to the Lukwangule Plateau at about 2634 m. The surveys were conducted between 2001 and 2003. Five altitudinal zones were chosen and surveyed intensively, including 1000, 1200, 1500, 2000, and 2500 m (Figure 1). The lowest forested site is found at 1200 m in the Shikurufumi Forest Reserve (Fig. 1). Shikurufumi Forest Reserve is a forest fragment at the foothill of the western slopes of the Uluguru South Mountains.

At 1000 m, surveys were conducted in September 2001 (dry season); and at 1200 m the surveys were conducted in March 2002 (wet season) and in August 2002 (dry season). At 1500 m, the surveys were conducted both in cultivated and forested areas. In the cultivated areas, surveys were done in September 2001; in forest, they were conducted in March 2002 and August 2002. At 2000 m, the surveys were conducted in September 2001 and March 2002, and at 2500 m, the surveys were conducted between March and April 2003 (wet season) and between June and July 2003 during the dry season. Details and locations of each site are given in Table 1.

Standard methods for surveying amphibians were used, including drift fences with pitfall buckets, plots, and audiovisual encounter surveys (Heyer et al., 1994). Six drift fences with pitfall buckets were set at each altitudinal zone for seven days. Each pitfall line consisted of 11 pitfall buckets set at 5-m intervals, and a drift fence of polythene bisected all of the buckets in the line (see Stanley et al., this volume). Pitfall lines were set to include different habitat types (i.e., cultivated areas, forests, forest edges, and grasslands). Buckets were checked at least once every day.

Pitfall lines cannot adequately sample all amphibians; they were supplemented with plot method and audio-visual encounter surveys. Ten plots of 5 by 5 m were established at each altitudinal zone. Plots were systematically set at each zone, and the interval between one plot and another was 50 m. Each plot was searched thoroughly for amphibians once every sampling season by four observers. Sampling involved searching for amphibians in leaf litter, between or within grass tussocks, on plant trunk and leaves, and by turning logs and stones. Digging underground (5-10 cm deep) was also done to ensure a thorough search. Audio-visual encounter surveys were conducted both during the day and night to detect amphibians not sampled by pitfall lines and plots. Amphibians found were identified and released after taking some voucher specimens. Material collected has been deposited in the Department of Zoology and Wildlife Conservation, University of Dar es

Salaam, Tanzania; Natural History Museum, London; and Museo Tridentino di Scienze Naturali, Trento, Italy. Species were classified following the taxonomy of Frost et al. (2006).

Data Analysis

Composition of amphibian species in different altitudinal zones was compared using the Jaccard Similarity Index (S_J) (Ludwig & Reynolds, 1988). This index uses presence/absence data and is widely used to assess similarity of communities. S_J is frequently multiplied by 100%, and may be represented in terms of dissimilarity (i.e., $D_J = 1.0$ & minus; S_J). The similarity index values range from 0 (no species common to both communities) to 1.0 (all species found in both communities). A higher similarity index suggests greater similarity of species among communities.

It is represented by the formula

$$S_{\rm J} = \frac{a}{(a+b+c+n)},$$

where S_J is the Jaccard similarity coefficient, *a* is the number of species common to (shared by) communities, *b* is the number of species unique to the first community, *c* is the number of species unique to the second community, and *n* is the number of species unique to community *n*.

Results

The study recorded a total of 21 amphibian species belonging to eight families on the western slopes of Uluguru South Mountains. Observations revealed differences in species composition at different altitudes. Certain species occurred at more than one altitudinal zone, whereas for some species, there was an altitudinal overlap.

Seven species were recorded at 1000 m, 12 species at 1200 m, 11 species at 1500 m, seven species at 2000 m, and five species at 2500 m. The pattern shows a general decrease in the number of species with increased altitude (Table 2). An exception is at 1000 m, which had fewer species than did 1500 m. Only one species (*Arthroleptis affinis*) was found to occur on all altitudinal zones on the western slopes of the Uluguru South Mountains from 1200 m and above. The submontane forest portion (800–1500 m) supported more amphibian species than montane or upper montane forest portions (Table 2).

The amphibian species compositions were clearly separated by altitude. The study sites that were adjacent to each other showed greater similarity in amphibian species composition than did sites distant from each other. Pairwise comparison of species composition between different altitudinal zones is as shown in Table 3.

Species Accounts

Family Arthroleptidae *Arthroleptis* spp.

This is one of the most taxonomically difficult genera in East Africa due to its variable coloration and morphology. Its

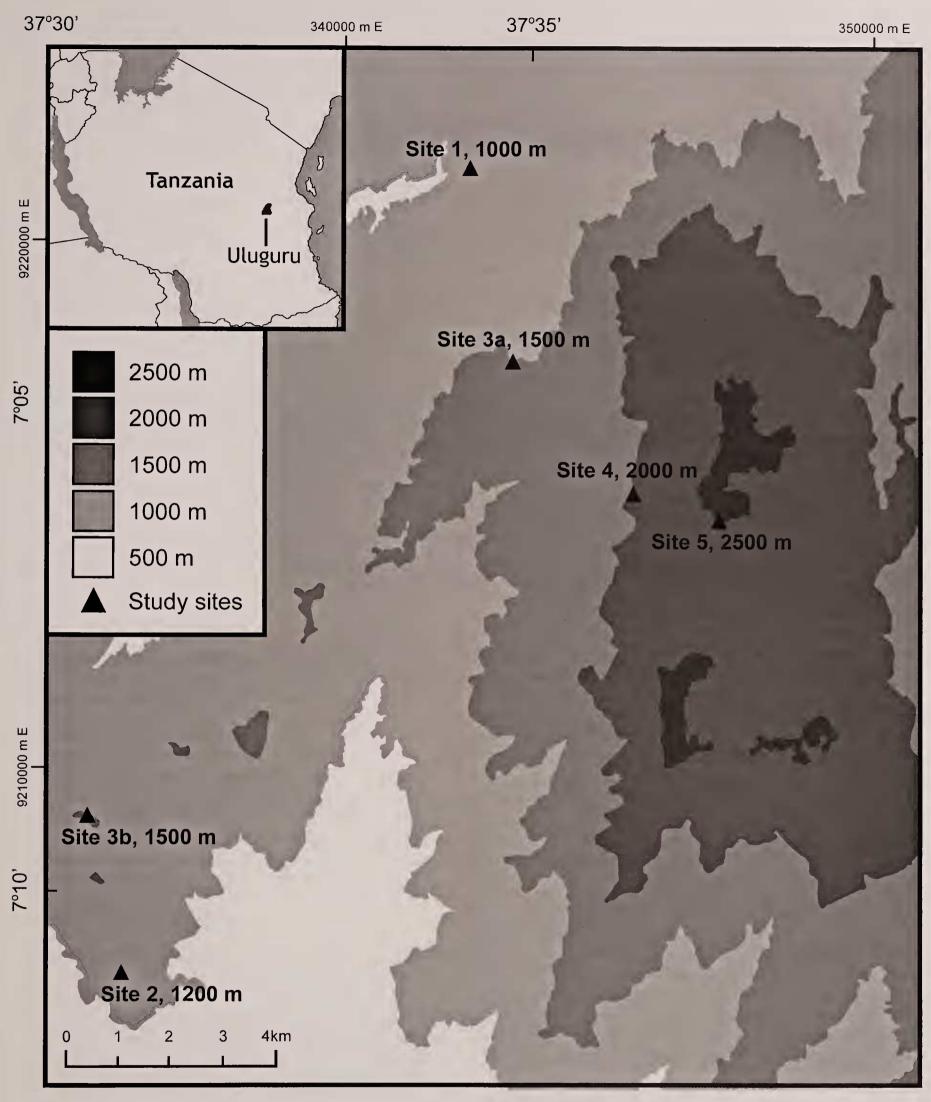


FIG. 1. Map of the western slopes of Uluguru South Mountains showing the study sites and elevations (Source: Tanzania Maps [Mgeta], Toposheet 201/1, Y742 Series, 1982).

taxonomy is not yet clearly settled. Breeding in known *Arthroleptis* species does not depend on water (Channing & Howell, 2006); members lay their eggs in nests under leaf litter and have no free-living tadpole stage.

Arthroleptis affinis Ahl, 1939

This species is widely distributed along the altitudinal gradient in the Uluguru South Mountains. It has a very

TABLE 1. Location of the study sites on the western slopes of the Uluguru South Mountains, Tanzania.

| Sampling site | Altitude (masl) ¹ | Coordinates | Sampling time | Habitat type | | |
|---------------|------------------------------|-------------------------|--|---------------------------------|--|--|
| 1 | 1000 | 7°3.844′S, 37°34.254′E | 1–10 September 2001 | Cultivated land | | |
| 2 | 1200 | 7°10.925′S, 37°30.744′E | 1–10 March 2002 12–22 August 2002 | Cultivated land and forest edge | | |
| 3a | 1500 | 7°5.155′S, 37°35.124′E | 12–21 September 2001 | Cultivated land | | |
| 3b | 1500 | 7°9.125'S, 37°30.565'E | 1–20 March 2002 12–22 August 2002 | Forest | | |
| 4 | 2000 | 7°6.350'S, 37°36.700'E | 23 September–2 October 2001 24 March–2 April 2002 | Montane forest | | |
| 5 | 2500 | 7°6.782'S, 37°36.850'E | 11 March–9 April 2003 24 June–17 July 2003 | Forest and grassland | | |

¹ masl, meters above sea level.

wide altitudinal range and occupies habitats from the forest and cultivated areas and from the lowest sites, at 1200 m, to the upper montane forests at 2500 m. This species is terrestrial, found mostly under or on leaf litter in the forest. In other Eastern Arc Mountains it is known to occur from 190 to 2104 m (Poynton & Loader, 2008).

Arthroleptis stenodactylus Pfeffer, 1893

Individuals of this species were found at 1000, 1200, and 1500 m (Table 4). This species inhabits the forest interior, forest edge, and cultivated areas. In forest, this species dwells mostly under leaf litter; large numbers of individuals were caught in pitfall buckets.

TABLE 2. Altitudinal distribution of amphibian species on the western slopes of the Uluguru South Mountains. X means species detected; blank means undetected.

| | | | Altitude (m) | | |
|---|--------|------------------|--------------|--------|--------|
| Family/Species | 1000 | 1200 | 1500 | 2000 | 2500 |
| Arthroleptidae | | | | | |
| Arthroleptis affinis Arthroleptis stenodactylus Arthroleptis xenodactyloides Leptopelis parkeri | X X | X X X | X X X | X X | Х |
| Brevicipitidae | | | | Α | |
| Breviceps mossambicus Callulina kreffti Probreviceps loveridgei Probreviceps uluguruensis Spelaeophryne metlineri | | X X X X | X X | х | х |
| Bufonidae | | | | | |
| Amietophrynus gutturalis Nectophrynoides viviparus Nectophrynoides laevis Nectophrynoides sp. | Х | Х | Х | X X | x x |
| Hyperoliidae | | | | | |
| Hyperolius puncticulatus Kassina senegalensis | Х | X X | Х | | |
| Phrynobatrachidae | | | | | |
| Plırynobatrachus natalensis Phrynobatrachus udzungwensis | Х | Х | X X | | |
| Ptychadenidae | | | | | |
| Ptychadena oxyrhynchus Strongylopus fuelleborni | Х | | | | Х |
| Pyxicephalidae | | | | | |
| Amietia angolensis | Х | Х | Х | Х | |
| Caeciliidae | | | | | |
| <i>Scolecomorplus uluguruensis</i> No. of species | 7 | 12 | X 11 | X 7 | 5 |

TABLE 3. Comparison of amphibian community similarity in different altitudinal zones (m) on the western slopes of Uluguru South Mountains using Jaccard's Index (S_J) .

| | 1000 | 1200 | 1500 | 2000 | 2500 | |
|--------------------------------------|------|-----------------|-------------------------------|------------------------------------|------|--|
| 1000 1200 1500 2000 2500 | 1 | 0.75 (75%) 1 | 0.67 (67%) 0.64 (64%) 1 | 0 0.14 (14%) 0.20 (20%) 1 | | |

Arthroleptis xenodactyloides Hewitt, 1933

Individuals of this species were found at 1000, 1200, and 1500 m (Table 4). It is a terrestrial species that inhabits both the leaf litter in the forest and cultivated areas.

Leptopelis parkeri Barbour & Loveridge, 1928

Leptopelis parkeri is a tree frog that inhabits the forest at an altitude of 2000 m. It was found within the leaf axils of wild bananas filled with water. Eggs, recovered with the adult frogs from the leaf axils of wild bananas, could be the eggs of Leptopelis. The eggs were small and pigmented; however, it is difficult to state with certainty that they were L. parkeri eggs without further investigation. This species exhibits sexual dimorphism. Males are grayish to brownish or olive green with a conspicuous yellow pattern forming irregular transverse bands; females possess a uniform olive-green dorsum.

Brevicipitidae

Breviceps mossambicus Peters, 1854

Individuals of this species were found in the cultivated areas at 1200 m, especially during the dry season, and were mainly found in the leaf litter.

Callulina kreffti Nieden, 1911

This species was recorded at 1200 and 1500 m. It was found both in forest and farmland habitats at 1500 m, and at 1200 m only in the forest edge. Individuals were found in rotten logs and leaf axils of wild and cultivated banana plants. Many individuals were either opportunistically collected or visually encountered; none were collected in pitfalls.

Probreviceps loveridgei Parker, 1931

Individuals of this species were found at 1200 and 1500 m in the Shikurufumi Forest Reserve. It inhabits both forested and cultivated areas at 1500 m, but only in the forest edge at 1200 m. Like many other leaf-litter frogs, breeding does not take place in the water. The females lay their eggs under leaf litter, and the young develop directly into adults (Müller et al., 2007). Eggs were recovered from the leaf litter throughout the study, indicating that this species breeds through the year.

Probreviceps uluguruensis (Loveridge, 1925)

This species was collected from 2000 m to the Lukwangule Plateau. It is endemic to the Uluguru Mountains and is found in leaf litter, underground chambers in the forest, and below grass tussocks on the Lukwangule Plateau. Morphologically, *Probreviceps uluguruensis* is highly variable in color and pattern.

Spelaeophryne methneri Ahl, 1924

Only a single adult female measuring 31 mm snout-vent length was collected over the entire sampling period in cultivated land at 1200 m.

Family Bufonidae

Amietophrynus gutturalis (Power, 1927)

Individuals of this species were found at lower altitudes at 1500 m and below (Table 4). This species is highly versatile; it can inhabit various habitat types from degraded forests, moist savanna, and agricultural areas to human settlements. In the study area, this species was restricted to the cultivated land. No *A. gutturalis* were recorded in the forest habitat throughout the study period. Males were found calling at night from wetter areas and ephemeral water pools in the cultivated land at 1000, 1200, and 1500 m. The calls intensified during the wet season, especially after rain.

Nectophrynoides laevis Menegon et al., 2004

This species is restricted to the upper elevations at 2000 m. *Nectophrynoides laevis* appears to have a restricted distribution in the Uluguru South Mountain forest and is only known from one specimen. Nothing is known about its breeding biology and breeding behavior (Menegon et al., 2004). It is a tree frog that inhabits the forest habitat and the type was found on vegetation about 1 m off the ground.

Nectophrynoides viviparus Tornier, 1905

In the Uluguru South, this species is restricted to the upper montane forest from 1900 m to the Lukwangule Plateau. Individuals were found under or on leaf litter and in grass tussocks on the plateau. They were also observed climbing and calling on vegetation to about 1 m off the ground. This species is highly variable in color pattern and morphology. Advertisement calls produced by frogs at 2000 and 2500 m differed dramatically. The advertisement call of the male recorded at 2000 m was low-pitched and composed of a sequence of 23 discrete notes. Mean call duration was 54 ms (range, 43-87, n = 3). The fundamental and dominant frequencies were dissimilar for each note at 1.698 and 1.727 kHz, respectively. Nectophrynoides viviparus from the Lukwangule Plateau (2500 m) has a characteristic call of high-pitched clicks, "cluck" "cluck," composed by a series of six to eight notes. Mean call duration was 475 ms (range, 128-833, n = 6) with fundamental and dominant frequencies of 2.386 and 2.427 kHz, respectively. The differences in calls suggest that the two forms may be distinct; this requires further investigation.

Nectophrynoides sp.

During the study, three specimens were collected in a forest patch on the Lukwangule Plateau. These individuals were distinct from other known taxa and may tentatively be considered new species. These were found in a hole in a standing dead tree. TABLE 4. Number of individuals of different amphibian species found during the surveys in different altitudinal zones (m) on the Uluguru South Mountains. Blank cells indicate no individuals of the species were detected.

| | 1000 | | 1200 | | 1500 | | 2000 | | 2500 | |
|--|---------|-----|---------|-------------------|--------|---------------|---------|---------|------|-----|
| Family/Species | Dry | Wet | Dry | Wet | Dry | Wet | Dry | Wet | Dry | Wet |
| Arthroleptidae Arthroleptis affinis Arthroleptis stenodactylus Arthroleptis xenodactyloides Leptopelis parkeri | 1 12 | | 31 6 | 6 36 17 | 4 6 | 5 11 12 | 2 25 | 15 7 | | 3 |
| Brevicipitidae Breviceps mossambicus Callulina kreffti Probreviceps loveridgei Probreviceps uluguruensis Spelaeopluyne metlmeri | | | 9 5 | 5 1 40 1 | 5 6 | 9 | 16 | 63 | 45 | 26 |
| Bufonidae Amietophrynus gutturalis Nectophrynoides viviparus Nectophrynoides laevis Nectophrynoides sp. | 9 | | 21 | 1 | 5 | 7 | 7 | 59 1 | 39 | 31 |
| Hyperoliidae Hyperolius puncticulatus Kassina senegalensis | 5 | | 14 | 22 1 | 4 | 27 | | | | |
| Phrynobatrachidae Phrynobatrachus natalensis Phrynobatrachus udzungwensis | 7 | | 1 | 10 | 1 | 27 12 | | | | |
| Ptychadenidae Ptychadena oxyrhynchus Strongylopus fuelleborni | 1 | | | | | | | | 27 | 128 |
| Pyxicephalidae Amietia angolensis | 8 | | 2 | 8 | 4 | 1 | 8 | 10 | | |
| Caeciliidae Scolecomorphus uluguruensis | | | | | | 3 | | 1 | | |

Family Hyperoliidae *Hyperolius puncticulatus* (Pfeffer, 1893)

This tree frog was recorded in cultivated areas at 1000 and 1200 m and at the forest edge at 1500 m but was not found in the forest interior. It is highly variable in color and pattern (Harper et al., 2010). Males were calling on vegetation about 0.5–1 m high above the ground near streams.

Kassina senegalensis (Duméril and Bibron, 1841)

This species was collected in pitfall buckets at forest edge at 1200 m during the wet season.

Family Phrynobatrachidae Phrynobatrachus natalensis (Smith, 1849)

This species was found at 1000, 1200, and 1500 m near stream banks in cultivated lands and at forest edge at 1500 m.

Phrynobatrachus uzungwensis Grandison & Howell, 1983

This species was only found in forest habitat during the wet season at 1500 m, specifically in the forest floor leaf litter. Breeding probably occurs in the rainy season. During this period many individuals were collected from the forest floor; none were collected in dry season.

Family Ptychadenidae

Ptychadena oxyrhynchus (Smith, 1849)

This species was collected in the degraded areas (cultivated areas) at 1000 m. It was found in abandoned farms dominated by grasses during the dry season.

Family Pyxicephalidae Amietia angolensis (Bocage, 1866)

This is a common, semi-aquatic species that occupied cultivated areas at 1000, 1200, and 1500 m to the forested habitat at 2000 m. It is highly associated with water, being found in rivers and along streams.

Strongylopus fuelleborni Nieden, 1911

This species is restricted to the Lukwangule Plateau grasslands in the Uluguru South Mountains ($\sim 2400-2500$ m). Most individuals were observed near water and only a few were found away from a water source. Males call from the grassland swamps and have a characteristic call of a high-

pitched "pip" uttered once or in a short burst of three or four. This species was removed from synonymy with *Rana merumontana* Lönnberg, 1910, by Poynton (2004).

Family Caeciliidae

Scolecomorphus uluguruensis Barbour & Loveridge, 1928

This caecilian was only found in forests from 1500 to 2000 m. Individuals were mostly captured in pitfall buckets and also found in plots during the wet season.

Discussion

A total of 21 species were recorded during this study. Four additional species of amphibians are known to occur in the Uluguru South Mountains but were not recorded during the study. These include: Nectophrynoides cryptus (Howell, 1993), N. pseudotornieri (at 2040 m; Menegon et al., 2004; Frontier Tanzania, 2005), Hoplophryne uluguruensis (at 2040 m; Frontier Tanzania, 2005), and Petropedetes yakusini (900-1820 m; Frontier Tanzania, 2005). The unrecorded species are perhaps rare or highly cryptic and therefore were not detected. Of the 25 amphibian species known from Uluguru South, five species, including N. cryptus, N. laevis, N. pseudotornieri, Probreviceps uluguruensis, and Scolecomorphus uluguruensis, are endemic to the Uluguru Mountains. The other five species found in the Uluguru, including Callulina kreffti, N. viviparus, P. loveridgei, P. yakusini, and Leptopelis parkeri, are endemic to the Eastern Arc Mountains in general (see Poynton et al., 2006). The Eastern Arc Mountains are known for high endemism in many taxonomic groups (Dinesen et al., 2001), explained as the consequences of stable local conditions (Burgess et al., 2007). These stable conditions are the result of historical processes in the Eastern Arc Mountains that would result in species replacement patterns that are congruent across many evolutionary lineages (Burgess et al., 2007).

The data indicate a general decline in the number of amphibian species with increasing elevation. The decline in amphibian species richness and diversity with an increasing elevation in tropical mountain forests has been reported across the globe (e.g., Brown & Alcala, 1961; Fauth et al., 1989). The decrease in temperature, precipitation, and productivity are thought to be the most critical factors limiting species diversity at higher elevations (Rahbek, 1995), although how the environmental variables impinge on the life of amphibians is not fully understood (Loader et al., 2004).

Many of the species found below 1500 m are widely distributed throughout lowland areas in East Africa (e.g., *Arthroleptis stenodactylus, A. xenodactyloides, Amietophrynus gutturalis,* and *Ptychadena oxyrhynchus*; see Channing & Howell, 2006), whereas those found above 1500 m, including *N. laevis N. viviparus, L. parkeri,* and *P. uluguruensis,* have a more restricted distribution. This shows distinctiveness of highland amphibian fauna from those at the lowland. Recent taxonomic studies elsewhere in the Eastern Arc Mountains have shown distinctiveness in some of the isolated populations, such as *Callulina* (Loader et al., 2010). In the Uluguru South Mountains, at least three species of *Nectophrynoides* are known, one of which, *N. viviparus,* was found at more than one altitudinal zone (Table 2). The calls of males at 2000 m were different from those at 2500 m, suggesting that the two

populations might be genetically distinct. Further investigation is needed to determine their status. The altitudinal limit for lowland and montane forest herpetofauna has been reported from other areas, including Kibale National Park (Vonesh, 2001), Mahenge Mountains (Loader et al., 2004), Udzungwa Mountains (Menegon & Salvidio, 2005), and across southern and eastern Africa (Poynton & Broadley, 1991; Poynton, 1992, 2003; Poynton & Boycott, 1996). According to Poynton et al. (2006), the differences between montane and lowland amphibian assemblages appear to be long standing, broadly characterized respectively by cool temperate relicts and widespread generalists rather than local elimination of species common to both.

The number of amphibian species at 1200 m was twice the number of species found at 1000 m. Sampling at 1000 m included cultivated areas in which all natural vegetation had been cleared and replaced by crops, whereas at 1200 m, sampling included both cultivated areas and forest edge. Most of the species found at 1200 m were forest-dependent species (Howell, 1993) that cannot tolerate disturbed habitats. Furthermore, the 1000-m zone was only sampled during the dry season, whereas the 1200-m zone was sampled during both dry and wet seasons. These reasons may explain the smaller number of species at 1000 than at 1200 m. The effect of habitat degradation on composition and diversity of species has been stated (Hillers et al., 2008). Cultivation in the Uluguru Mountains is normally associated with the removal of plant cover, affecting the thickness of leaf litter, humidity, and canopy cover. Species like Probreviceps loveridgei, Spelaeopluryne methneri, and Breviceps mossambicus were found at 1200 m but not at 1000 m. These species are commonly associated with leaf litter (Channing & Howell, 2006); it seems human-induced clearance of fields at 1000 m may have eliminated them. Hillers et al. (2008) showed that opening the canopy changes the microclimate and most likely exceeds the physiological capability of several frog species, and this can lead to a reduction in diversity of amphibian species. This study demonstrates rather restricted habitat and altitudinal distribution of some montane endemics, which raises conservation concerns, especially as the increasing loss of habitat at lower altitudes and, continuing toward higher altitudes, will eventually eliminate some species.

Acknowledgments

This study has been made possible by the financial support of DANIDA-Enreca Biodiversity Project. The Catchment Forest Office, Morogoro Region, granted permission to work in the Uluguru South Forest Reserve. We thank Prof. Kim Howell and Prof. A. Nikundiwe of the Department of Zoology and Wildlife Conservation, University of Dar es Salaam, for their input during the study. We are grateful to Dr. F. Urasa and Dr. C. Msuya of the Department of Zoology and Wildlife Conservation. University of Dar es Salaam, for their logistical support during field work. We also extend our thanks to Prof. J. C. Poynton of the Natural History Museum, London, and Prof. A. Channing of the University of Western Cape, South Africa, for assisting in identification of the specimens. The authors thank Dr. S. P. Loader and W. T. Stanley for providing helpful comments during the preparation of this paper. Rebecca Banasiak helped prepare Figure 1.

Literature Cited

- BARBOUR, T., AND A. LOVERIDGE. 1928. A comparative study of the herpetofauna of the Uluguru and Usambara Mountains, Tanganyika Territory with description of new species. Memoirs of the Museum of Comparative Zoology, **50**: 87–265.
- BROWN, W. C., AND A. C. ALCALA. 1961. Populations of amphibians and reptiles in the submontane and montane forests of Cuernos de Negros, Philippine islands. Ecology, **42**: 628–636.
- BUCKLEY, L. B., AND W. JETZ. 2007. Environmental and historical constraints on global patterns of amphibian richness. Proceedings of the Royal Society B: Biological Sciences, 274: 1167–1173.
- BURGESS, N. D., T. M. BUTYNSKI, N. J. CORDEIRO, N. H. DOGGART, J. FJELDSÅ, K. M. HOWELL, F. B. KILAHAMAA, S. P. LOADER, J. C. LOVETT, B. MBILINYI, M. MENEGON, D. C. MOYER, E. NASHANDA, A. PERKIN, F. ROVERO, W. T. STANLEY, AND S. N. STUART. 2007. The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. Biological Conservation, 134: 209–231.
- CHANNING, A., AND K. M. HOWELL. 2006. Amphibians of East Africa. Cornell University Press, Ithaca, New York.
- DAVIS, F. W., D. M. STORMS, J. E. ESTES, J. SCEPAN, AND J. M. SCOTT. 1990. An information systems approach to the preservation of biological diversity. International Journal of Geographical Information Systems, 4: 55–78.
- DINESEN, L., T. LEHMBERG, M. C. RAHNER, AND J. FJELDSÅ. 2001. Conservation priorities for the forests of the Udzungwa Mountains, Tanzania, based on primates, duikers and birds. Biological Conservation, **99:** 223–236.
- DOGGART, N. J., J. LOVETT, B. MHORO, J. KIURE, AND N. D. BURGESS. 2004. Biodiversity surveys in the forest reserves of the Uluguru Mountains: An overview of the biodiversity of the Uluguru Mountains. Tanzania Forest Conservation Group, Dar es Salaam, Tanzania.
- FAUTH, J. E., B. I. CROTHER, AND J. B. SLOWINSKI. 1989. Elevational patterns of species richness, evenness and abundance of the Costa Rican leaf-litter herpetofauna. Biotropica, **21**: 178–185.
- FRONTIER-TANZANIA. 2005. Uluguru component biodiversity survey 2005, vol. 2: Uluguru South Forest Reserve. In Bracebridge, C., E. Fanning, K. M. Howell, P. Rubio, and F. A. V. St. John, eds., Frontier-Tanzania Environmental Research Report 118. Available at: http://www.frontier-publications.co.uk/reports/Tanzania/Forest/Ulugurus2004/FTER118UluguruSouthForestReserveII.pdf (15 September 2010).
- FROST, D. R., T. GRANT, J. FAIVOVICH, R. H. BAIN, A. HAAS, C. F. B. HADAD, R. O. DE SA, A. CHANNING, M. WILKINSON, S. C. DONNELLAN, C. J. RAXWORTHY, J. A. CAMPBELL, B. L. BLOTTO, P. MOLER, R. C. DREWES, R. A. NUSSBAUM, J. D. LYNCH, D. M. GREEN, AND W. C. WHEELER. 2006. The Amphibian Tree of Life. Bulletin of the American Museum of Natural History Number 297, New York.
- HARPER, E. B., G. J. MEASEY, D. A. PATRICK, M. MENEGON, AND J. R. VONESH. 2010. Field Guide to the Amphibians of the Eastern Arc Mountains and Coastal Forests of Tanzania and Kenya. Camerapix Publishers International, Nairobi, Kenya.
- HEATWOLE, H. 1982. A review of structuring in herpetofaunal assemblages, pp. 1–19. In Scott, N. J., Jr., ed., Herpetological Communities. A Symposium of the Society for the Study of Amphibians and Reptiles and the Herpetologists League August 1977, U.S. Fish and Wildlife Service, Wildlife Research Report 13, Washington DC, pp 1–19.
- HEYER, W. R., M. A. DONNELLY, R. W. MCDIARMID, L. C. HAYEK, AND M. S. FOSTER. 1994. Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians. Smithsonian Institution Press, Washington, D.C.
- HILLERS, A., M. VEITH, AND M. O. RÖDEL. 2008. Effects of forest fragmentation and habitat degradation on West African leaf-litter frogs. Conservation Biology, **22**: 762–772.
- HOWELL, K. M. 1993. Herpetofauna of the African forests, pp. 173– 202. In Lovett, J. C., and S. K. Wasser, eds., Biogeography and Ecology of the Rain Forests of Eastern Africa. Cambridge University Press, Cambridge, United Kingdom.

- LOADER, S. P., D. J. GOWER, W. NGALASON, AND M. MENEGON. 2010. Three new species of *Callulina* (Amphibia: Anura: Brevicipitidae) highlight local endemism and conservation plight of Africa's Eastern Arc forests. Zoological Journal of the Linnean Society, 160: 496–514.
- LOADER, S. P., J. C. POYNTON, AND J. MARIAUX. 2004. Herpetofauna of Mahenge Mountain, Tanzania: A window on African biogeography. African Zoology, **39:** 71–76.
- LOVETT, J. C. 1990. Classification and status of the moist forests of Tanzania. Hamburg 1990, Symposium. Mitteilungenaus den Institut fur Allgemeine Bootanik Hamburg, **23**: 287–300.
- ------. 1993. Eastern Arc moist forest flora, pp. 33–56. *In* Lovett, J. C., and S. K. Wasser, eds., Biogeography and Ecology of the Rain Forests of Eastern Africa. Cambridge University Press, Cambridge, United Kingdom.
- LUDWIG, J. A., AND J. F. REYNOLDS. 1988. Statistical Ecology: A Primer on Methods and Computing. John Wiley, New York.
- MENEGON, M., AND S. SALVIDIO. 2005. Amphibian and reptile diversity in the southern Udzungwa Scarp Forest Reserve, south-eastern Tanzania, pp. 205–212. *In* Huber, B. A., B. J. Sinclair, and K. H. Lampe, eds., African Biodiversity: Molecules, Organisms, Ecosystems, Proceedings of the 5th International Symposium on Tropical Biology. Museum Koenig, Bonn.
- MENEGON, M., S. SALVIDIO, AND S. P. LOADER. 2004. Five new species of *Nectophrynoides* Noble 1926 (Amphibia: Anura: Bufonidae) from the Eastern Arc Mountains, Tanzania. Tropical Zoology, **17**: 97–121.
- MÜLLER, H., S. P. LOADER, W. NGALASON, K. M. HOWELL, AND D. J. GOWER. 2007. Reproduction in Brevicipitid frogs (Amphibia: Anura: Brevicipitidae)—evidence from *Probreviceps m. macrodac-tylus*. Copeia, **3**: 728–734.
- MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. DA FONSECA., AND J. KENT. 2000. Biodiversity hotspots for conservation priorities. Nature, **403**: 853–858.
- OWEN, J. G. 1989. Patterns of herpetofaunal species richness: Relation to temperature, precipitation and variance in elevations. Journal of Biogeography, 16: 141–150.
- Pócs, T. 1976a. The role of epiphytic vegetation in the water balance and humus production of the rain forests of the Uluguru mountains, East Africa. Boissiera, **24**: 499–503.
- ——. 1976b. Bioclimatic studies in the Uluguru mountains (Tanzania, East Africa) II. Correlations between orography, climate and vegetation. Acta Botanica Academiae Scientiarum Hungaricae, **22**: 163–183.
- ——. 1976c. Vegetation mapping in the Uluguru mountains (Tanzania, East Africa). Boissiera, **24:** 477–498.
- POYNTON, J. C. 1962. Zoogeography of eastern Africa: An outline based on anuran distribution. Nature, 194: 1217–1219.
- Africa: Investigation by means of a Bloemfontein–Durban transect. Journal of the Herpetological Association of Africa, **40**: 2–8.
- African Journal of Herpetology, **49:** 33–41.
- . 2003. Altitudinal species turnover in southern Tanzania shown by anurans: Some zoogeographical considerations. Systematics and Biodiversity, 1: 117–126.
- -------. 2004. Stream frogs in Tanzania (Ranidae: *Strongylopus*): The case of *S. merumontanus* and *S. fuelleborni*. African Journal of Herpetology, **53**: 29–34.
- POYNTON, J. C., AND R. C. BOYCOTT. 1996. Species turnover between Afromontane and eastern African lowland faunas: Patterns shown by amphibians. Journal of Biogeography, 23: 669–680.
- POYNTON, J. C., AND D. G. BROADLEY. 1991. Amphibia Zambesiaca 5. Zoogeography. Annals of the Natal Museum, **32**: 221–277.
- POYNTON, J. C., AND S. P. LOADER. 2008. Clinal variation and its taxonomic consequences in the common Tanzanian forest frog, *Arthroleptis affinis*. Copeia, **3:** 517–526.

- POYNTON, J. C., S. P. LOADER, E. SHERRATT, AND B. T. CLARKE. 2006. Amphibian diversity in East African biodiversity hotspots: Altitudinal and latitudinal patterns. Biodiversity and Conservation, 16: 1103–1118.
- RAHBEK, C. 1995. The elevational gradient of species richness. A uniform pattern? Ecography, 18: 200–205.
- SCOTT, N. J. 1976. The abundance and diversity of the herpetofauna of tropical forest litter. Biotropica, 8: 41–58.
- STANLEY, W. T., S. M. GOODMAN, AND R. HUTTERER. 2011. Small mammal inventories in the East and West Usambara Mountains, Tanzania. 2. Families Soricidae (shrews) and Macroscelididae (elephant shrews), pp. 18–32. *In* Stanley, W. T., ed., Studies of montane vertebrates of Tanzania. Fieldiana: Life and Earth Sciences, Vol. 4.
- VONESH, J. R. 2001. Natural history and biogeography of the amphibians and reptiles of Kibale National Park, Uganda. Contemporary Herpetology, **4:** 123–135.